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CHANGES IN BIOMASS OF PENULTIMATE-INSTAR CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE) HUNTING ON FLOWERS LATE IN THE SUMMER

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ABSTRACT. Penultimate-instar crab spiders *Misumena vatia* foraging on goldenrod *Solidago* spp. in late summer gained mass slowly, averaging 0.8 mg/day, and usually did not molt into the adult stage before the end of the summer. In contrast, adults gained mass rapidly at this site, averaging 8.8 mg/day, taking larger prey and taking them more often than penultimates. The penultimates' prey consisted primarily of small flies, bees and wasps, and overlapped broadly with those of the adults, but did not include the most important resource of the adults, bumble bees, upon which the adults registered most of their gain. Penultimates captured prey biomass at only one-tenth the rate of the adults, and one-third the rate of adults per unit body mass.

Most studies of foraging animals have focused on adults (Morse 1980; Pyke 1984; Stephens & Krebs 1986), even though preadult stages may occupy the majority of many species' lifetimes. Proponents argue that this approach addresses the stage that contributes directly to reproduction, permitting the most ready estimation of fitness (see Lewontin 1978; Maynard Smith 1978). However, foraging events earlier in the life-cycle may affect one's success as an adult (Morse 1980; Skelly & Werner 1990; Fraser & Gilliam 1992), and lack of early success may result in many individuals not even surviving to the adult stage (e. g., Forrest 1987). Thus, information is needed on immature stages to compare with adult success, to determine how well adult foraging success describes foraging success in general (see Stein & Magnuson 1976; Sih 1982), and to establish how foraging repertoires vary over a range of sizes and ages.

Different life-cycle stages may vary in their proficiency at capturing a given kind of prey. This pattern is clearly illustrated by the success of the semelparous crab spider *Misumena vatia* Clerck (Thomisidae) at capturing bumble bees (*Bombus* spp.), which only adult females can subdue (Morse, unpubl. data). This prey is critical to fitness – without bumble bees, adult females seldom if ever gain enough mass to lay their single clutch of eggs (Fritz & Morse 1985).

Stages lacking similarly profitable prey will grow slowly, and molting and maturation may be greatly extended (Levy 1970). In addition to dangers resulting from increased time spent as a juvenile, slow growth may make such individuals vulnerable to critical seasons that can act as bottlenecks. For instance, many species of spiders do not overwinter as adults (e. g., Schaefer 1977), including *Misumena* (Morse unpubl. data). To evaluate growth patterns of a stage without access to extremely profitable prey, I gathered data on the activity patterns, prey capture, and rate of gain in mass of penultimate female *Misumena*, which cannot capture bumble bees. The results permitted me to compare the success of these penultimates with adult female *Misumena*, whose foraging and growth patterns my colleagues and I have studied in detail (Morse 1979, 1981, 1986, 1988; Morse & Fritz 1982, 1987; Fritz & Morse 1985; Kareiva, Morse & Eccleston 1989). For direct comparison, I also gathered similar data on the small number of prereproductive adult females present in the study area at the same time. Most adult females had already laid their eggs and were guarding them at that time (Morse 1987).

I conducted this study during late summer on *Misumena* that frequented goldenrods *Solidago* spp., the dominant native flowering plants in eastern North America at this time of year. Goldenrods are the principal foraging sites for *Misumena* at this season (Morse 1981, 1993). In the absence of an "ideal" prey for the penultimates, comparable to bumble bees for the adults, one may predict a relatively slower growth rate from the penultimates than from adults.

CHARACTERISTICS OF *MISUMENA*

The semelparous crab spider *Misumena vatia* (Thomisidae) has a life cycle of one year or more.

These spiders frequent flowers that attract large numbers of their insect prey. Typically, adult females lay their single clutch of 75–350 eggs during mid- or late summer, with extremes of early July to early September (Morse & Fritz 1982; Fritz & Morse 1985). Females guard their eggs in nests constructed from leaves, often until the young emerge nearly a month later (Morse 1987). Young overwinter as immatures in the litter, usually as third to sixth instars, but with less frequent penultimates and second instars. Some individuals probably overwinter more than once, but I have no evidence that they overwinter as adults. To date I have not recovered in the following spring any of the more than 300 marked adults (over a period of 15 field seasons) that did not lay eggs in the fall (Morse unpubl. data). [Neither have I recovered in the following spring any of the 1400+ egg-layers I have studied (Morse 1994) during this time.] Following wintering, these spiders hunt on flowers for insect visitors. Females subsequently grow rapidly if they find hunting sites that attract many large insect prey, sometimes increasing as young adults by as much as an order of magnitude (40 mg to 400 mg) within as little as two–three weeks (Fritz & Morse 1985). Penultimate females range from about 18 mg to 75 mg or more (Holdsworth & Morse in press), and can be readily separated from adults by the absence of red dorsolateral stripes on their abdomens (Gertsch 1939). Males are strikingly smaller than females, seldom exceeding 7 mg, and averaging 3–5 mg (Holdsworth & Morse in press).

METHODS

I carried out this study in a one ha field in Bremen, Lincoln County, Maine. The field is covered by a variety of grass species, with considerable numbers of forbs scattered throughout. During late July and August 1981, when this study was conducted, goldenrod was the dominant flowering forb. The principal species of goldenrod, blooming in sequence, were *Solidago juncea*, *S. canadensis*, and *S. rugosa*. They will be considered collectively for the purposes of this study. Clonal in nature, these goldenrods typically exhibit a clumped distribution, with 10–75 flowering stems per site in the study area. This site is described in further detail elsewhere (Morse 1979, 1981).

I used 45 immature female *Misumena* in this study, which, at 18–34 mg, were almost certainly all in the penultimate instar. [In another study, all 49 females of this size range captured in the field and subsequently reared through to their next molt assumed adult condition at 31 mg or more, with a mean of 54.7 mg ± 12.5 SD (Holdsworth & Morse unpubl. data).] These penultimates were added to the study as found, thus Day 1 of observations was not the same for all individuals.

I gathered data simultaneously on a sample of eight prereproductive adult females, all of these individuals I could find in the study area at this time. The small sample size of adults deserves note. Numbers of these individuals were extremely low in the study area, and the failure of additional small, prereproductive adult females to appear during the study period strongly suggested that very little, if any, recruitment occurred from the pool of penultimate females into the adult population.

Spiders were initially given a unique number, placed on the abdomen, using indelible ink. They were then weighed on a Kahn Electrobalance, returned to their sites on goldenrod and censused for presence, location, and prey capture at least every two hours during the daytime for periods of up to two weeks. Repeat weighings were made for 13 of the penultimate individuals and six of the adults at intervals averaging three–four days. Visits at two-hour intervals ensured that I recorded nearly all of the diurnal prey that the spiders captured (Morse 1979, 1981). Any nocturnal captures, which are infrequent on goldenrod and confined to moths taken by adults (Morse 1981), could be detected by the presence on the following morning of carcasses still being fed on or recently discarded (Morse 1981).

The penultimate spiders were divided into three groups on the basis of the information gathered upon them: 1) weighed two (3), three (7) or four (3) times and observed for several days (5–12 days); 2) weighed once and observed more than one day (3–11 days); and 3) weighed once and observed for a single day. As a result, some of these individuals provide more information than others. Six of the adult females met the criteria of Category 1 (3–13 days) and the other two of Category 2 (2–6 days). Adults in Category 1 were weighed two (1), three (4), or four (1) times.

Insect prey were recorded and assigned to group (usually order, but species in case of principal prey) and size category. Routine weighings of fresh specimens of these species (Morse unpubl. data) permitted rough estimates of prey biomass at time of capture. Although ingested biomass

Table 1.—Characteristics of penultimate and adult female spiders. First two variables drawn from entire sample of individuals; last three variables drawn from sample that was weighed two or more times.

	Penultimates			Adults		
	$\bar{x}$ ± SD	*N*	Range	$\bar{x}$ ± SD	*N*	Range
Time between first two moves (days)	4.0 ± 3.0	24	1–11	5.3 ± 3.6	8	1–13
Distance of moves (cm)	50.0 ± 52.4	24	10–200	40.8 ± 15.8	4	25–60
Gain in mass (mg/day)	0.8 ± 0.5	13	−0.2–24	8.8 ± 6.2	6	−0.8–22.3
Gain in mass (%/day)	3.0 ± 2.4	13	−0.9–10.3	9.1 ± 5.5	6	−1.0–16.8
Time observed (days)	9.0 ± 2.0	13	7–12	6.5 ± 3.6	6	3–13

would have permitted a more precise measure of prey intake, it was impossible to capture and weigh the free-ranging prey before the spiders caught them. However, an earlier study (Morse 1979) demonstrated that adult female *Misumena* extracted very similar proportions of the smallest and largest prey items exploited by spiders in this study (57.5% of the *ca.* 4 mg syrphid fly *Toxomerus marginatus* and 57.1% of *ca.* 150 mg bumble bees *Bombus* spp.). Therefore, use of the wet masses of prey species should provide an acceptable estimate for comparisons. Biomass captured (estimated cumulative wet mass of all prey) was divided by total days of observation to determine the rate at which spiders obtained resources. I determined gains in mass from the spiders I weighed more than once. Rates of gain were established by dividing the total change in mass between the first and last weighings by the days elapsed.

RESULTS

Penultimate spiders weighed twice or more and observed several days initially weighed 25.4 mg ± 6.1 SD; those weighed once and observed more than one day weighed 24.9 mg ± 5.3 SD; and those weighed and observed one day weighed 23.2 mg ± 4.5 SD. These three groups did not differ in mass ($H = 0.891$, $df = 2$, $n = 45$, $P > 0.5$ in a Kruskal-Wallis one-way ANOVA). Therefore, I treated them as members of a single group for each variable about which they yielded data.

Gains of penultimates were slow, though variable, averaging 3% of their body mass per day (Table 1). In these individuals the mean increase amounted to 0.8 mg/day. At this rate they would gain an average of 24 mg/month, one month being the maximum possible time remaining with substantial numbers of flowers in bloom as hunting sites and temperatures favoring prey activity. Two of the 13 individuals even lost a small amount of mass (0.4, 0.9% of initial mass/day), falling from 23 to 22 mg over nine days, and from 24 to 22 mg over 11 days, respectively. The remainder gained from 0.5 to 10.3%/day, with only three of the individuals increasing over 1.0 mg/day. The two fastest gainers increased from 23 to 42 mg in eight days, and 23 to 40 mg in 11 days, respectively. Original mass and subsequent gain of this group of 13 spiders were not significantly correlated ($r_s = -0.316$ in two-tailed Spearman Rank Correlation Coefficient, $n = 13$, $P > 0.2$).

The penultimates' gains in mass can be compared with those of the adult females occupying the same flowers (Table 1). The adults, which weighed nearly four times as much as the penultimates (94.2 mg ± 29.8 SD, $n = 8$), gained mass 10 times more rapidly than penultimates and, as a function of gain per unit mass, three times more rapidly than penultimates (Table 1). These differences were both significant ($P = 0.01$ in two-tailed Mann-Whitney *U* Tests). Two of these adult females more than doubled their original mass, in 7 and 13 days, respectively; none of the penultimates exhibited such large relative gains. [Original mass and subsequent gain were not correlated in this sample ($r_s = -0.236$ in a two-tailed Spearman Rank Correlation Coefficient, $n = 6$, $P > 0.2$).]

This difference in uptake of mass mirrored the adults' superiority in total numbers of prey captured per unit time ($G = 6.89$, $df = 1$, $P < 0.01$ in a *G*-Test: Table 2) and size of prey captured ($P < 0.01$ in a Mann-Whitney *U* Test: Table 2). Notwithstanding the pronounced difference in gain of mass by adults and penultimates, they did not differ significantly in either the frequency with which they changed goldenrod inflorescences (Table 1; $P > 0.7$ in a two-tailed Mann-

Table 2.—Prey captured on goldenrod by penultimate and adult female spiders.

	Penultimate (n = 45)			Adult (n = 8)	
Prey	Mass (mg)	Number caught	Total (mg)	Number caught	Total (mg)
Toxomerus marginatus (Syrphidae)	4	13	52	1	4
Other small Diptera	8	6	48	2	16
Medium Diptera	15	1	15	2	30
Small bee	10	4	40	3	30
Small wasp	10	4	40	3	30
Butterfly	15	1	15	0	0
Moth	125	0	0	1	125
Bumble bee (*Bombus* spp.)	150	0	0	4	600
Spider (Salticidae)	10	0	0	1	10
Total	—	29	210	17	845
Total spider days		228		53	
Capture/day (mg)		0.92		15.9	
Size of item (mg)		7.2		49.7	

Whitney U Test) or in the distance that they moved at such times (Table 1; $P = > 0.5$, same test). Prey species taken by penultimates and adults overlapped broadly, but the penultimates did not capture any bumble bees, the major source of prey gain for the adults.

DISCUSSION

Although the critical data set is small, adult and penultimate female spiders differed markedly in their energetics during the late summer. The low rate of gain in mass suggests that many of the penultimate instars (probable minimum of 9 out of 13) would not reach the size at which they would likely molt into the adult stage (mean = 55 mg, minimum = 31 mg: see Methods) while foraging on goldenrod. Even those that grew large enough to molt to the adult stage would be very unlikely to grow large enough to lay a clutch of eggs. I have never found *Misumena* laying a clutch in the field if they weighed less than 114 mg (Fritz & Morse 1985; Morse unpubl. data). That few penultimates did molt into adults during this period is further suggested by the small numbers of prereproductive adult females present at that time (n = 8) and the extremely low rate at which additional small prereproductive adults were found over the study period.

This growth pattern of penultimates contrasts with the small cohort of adults observed at this time, which gained considerable mass as a result of capturing bumble bees, a prey that lies beyond the size range available to the penultimates. Adults in another study on goldenrod also gained mass rapidly (Morse 1981), a trait observed earlier in the summer on other species of flowers as well (Morse 1981; Fritz & Morse 1985). The penultimates' slow growth also contrasts with the success observed for early-instar *Misumena* on goldenrod, which recruit regularly onto this flower from their nests (Morse 1993), and frequently increase in mass several fold as a result of feeding on the small Diptera that frequent goldenrod flowers.

In this northerly clime, penultimates have at most a month of feeding time left before temperatures decline abruptly (early to mid-September), and an even shorter time before the last goldenrods senesce (late August–early September). Following the disappearance of the last goldenrod flowers in early September, only scattered asters (*Aster* spp.) remain, such that the opportunities for successful hunting decline markedly for these flower-frequenting individuals. These factors further decrease the possibility that many of them will molt into the adult stage before the end of the season. Their slow rate of growth will therefore relegate them to a second overwintering, which potentially entails further mortality. These spiders will, however, presumably be among the first to molt into the adult stage during the following spring and early summer and the first to lay their eggs in midsummer. Had they realized a rate of gain in body mass proportional to that of the adults on goldenrod (also see Morse 1981 for comparable success rates of adults on goldenrod), many would probably have molted into the adult stage at this time. Even this increase would, however, have consigned them to a close race to produce a clutch of eggs by the end of the season. Since I have, to date, no evidence of adult *Misumena* surviving over winter, increase in size and subsequent molt would have likely obviated an opportunity to reproduce. If they did succeed in laying a clutch, it, too, might be vulnerable to cold damage. If such clutches do reach the hatching stage, the success of the earliest instars is open to question. Second-instar young are extremely vulnerable to starvation, at least earlier in the season (Vogelei & Greissl 1989; Morse 1993). Further, the numbers of adult males at this season become extremely low (Holdsworth & Morse in press), so the possibility of an unfertilized clutch among late-developing adults at this season is high. Thus, in spite of the dangers of the impending winter, the penultimates' slow gains in mass on goldenrod may be more advantageous than they first appear. The penultimates' slow rate of gain may even allow them to accommodate for a natural "bottleneck" of the seasons. Their failure to change sites more rapidly or to move farther than adults at these times (Table 1) does not suggest that they are responding at this time to a perceived food shortage in a way characteristic of most animals, including adult *Misumena* (Morse & Fritz 1982).

Although the exact basis for molt into the adult stage is not known for *Misumena*, nutrition, size and growth rate are very likely to be critical environmental factors in terrestrial arthropods (Blakely 1981; Forrest 1987; Nijhout 1994). The marginal size (for molt) and slow growth rate characterizing these penultimates should be strong factors prolonging the onset of molt.

The results do not justify arguing at this time that the penultimates deliberately ration their rate of intake. However, as suggested by both Miyashita (1969) and Wise (1976), low availability of food late in the season may facilitate the delay of maturity in species that do not overwinter as adults.

Some arthropods are intrinsically programmed to suspend maturation in the latter part of summer. For example, the pitcher-plant mosquito *Wyeomia smithii* does not proceed into the last instar under decreasing photoperiods, which signify the return of winter conditions before the mosquito can complete its reproductive period and its offspring can reach an overwintering stage (Istock 1981).

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